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The development of earthworm populations following manipulation of the canopy leaf litter in a beechwood on limestone

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With 6 figures

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1. Introduction

In forest ecosystems the major source of nutrients and energy for the decomposer community of the soil subsystem is the input of canopy leaf litter (SCHAEFER, 1982).

This nutritive supply may be considered from two points of view: at the community level it can be regarded as an ultimate driving variable of overall community structure (productivity hypothesis of species diversity, CONNEL & ORIAS, 1964), while at the population level it may be a proximate limiting factor. These working hypotheses may be reformulated as questions:

(i) does the amount of leaf litter input influence the structure of the decomposer community?

(ii) does the amount of leaf litter input influence the abundance of decomposer species? These questions were investigated in a field experiment, which monitored the development of decomposer species following multiplication and exclusion of canopy leaf litter input.

In this paper, data on the population dynamics of lumbricid earthworms following experimental manipulations are presented. The corresponding changes in earthworm community structure are described by JUDAS (1989).

2. Material and methods

The study site was situated on the plateau of the "Göttinger Wald", a submontane beechwood on limestone (410–420 m a.s.l., 10°2'E 51°31'N), phytosociologically described as a Melico-Fagetum, subassociation of *Lathyrus vernus* (DIERSCHKE & SONG, 1982).

Adjacent 100 m^2-plots were used as experimental areas and controls as follows (cf. fig. 1):

(i) litter multiplication (**L5**): on two plots an additional input of four times the natural rate was added in November 1981 and 1982;
(ii) litter exclusion (**L0**): on four plots autumnal litter fall was excluded every year starting in 1981;
(iii) controls (**L1**): eight neighbouring plots were used as controls without manipulation of litter fall.

From April 1982 to April 1987 the density of lumbricid populations was determined at three month intervals for all treatments (with four interruptions) by 6–12 samples per treatment. For each sampling date two plots per treatment and three (or six) 1 m^2-squares per plot were chosen for sampling. Sampling squares were chosen by restricted randomization: central squares of the 100 m^2-plots were not used for the first years in order to minimize disturbance by the sampling procedure. The same 1 m^2-squares were used to sample earthworms, other faunal groups, and soil/litter chemical and physical parameters.

Methods used were hand-sorting of 0.1 or 0.0625 m^2 soil and litter samples (3–20 cm deep, depending on depth of stones and roots) and additional formalin extraction of deeper soil layers. Since October 1983 the litter fraction was extracted with a washing-sieving apparatus (cf. JUDAS 1988). Biomass of earthworms was determined on four sampling dates per year in 1983 (direct determination of ash-free dry mass); in

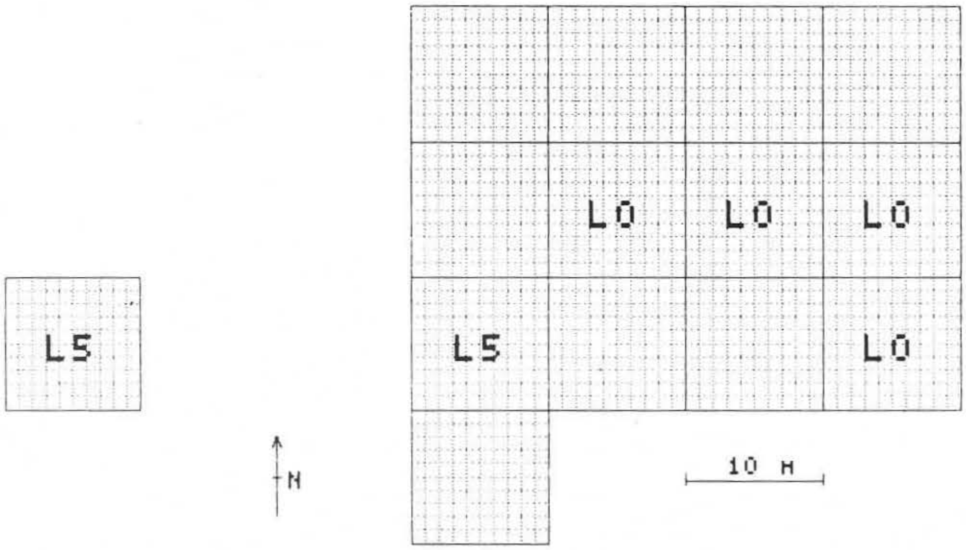


Fig. 1. Experimental design of leaf litter input manipulations: arrangement of 100 m^2-plots with multiplication (2*L5) or exclusion (4*L0) and 8 control plots.

1986 it was estimated from biovolume which was converted to ash-free dry mass by regression equations from NORDSTRÖM & RUNDGREN (1972).

Data on water content of soil and litter, litter standing crop, and soil temperature were obtained by standard methods and are provided for 1982 to 1984.

For the practical reason of avoiding sampling damage to the experimental area, the experimental design was not as optimal as demanded by HURLBERT (1984). In the analysis, manipulations and controls are compared after pooling treatment plots.

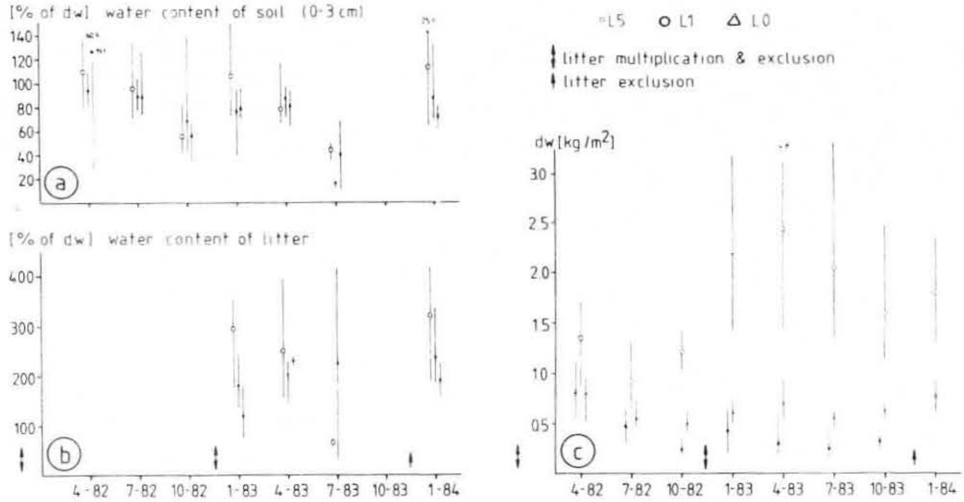


Fig. 2. Change of abiotic parameters following leaf litter input manipulations: water content of soil (a) and litter (b), total litter standing crop (c). Means and range of 2–6 samples of 357 cm^2 (litter standing crop) or 23.75 cm^2 (water content) are given for controls (L1), multiplication (L5) and exclusion (L0) in the first two years of the experiment. □ L5, ○ L1, ▲ L0.

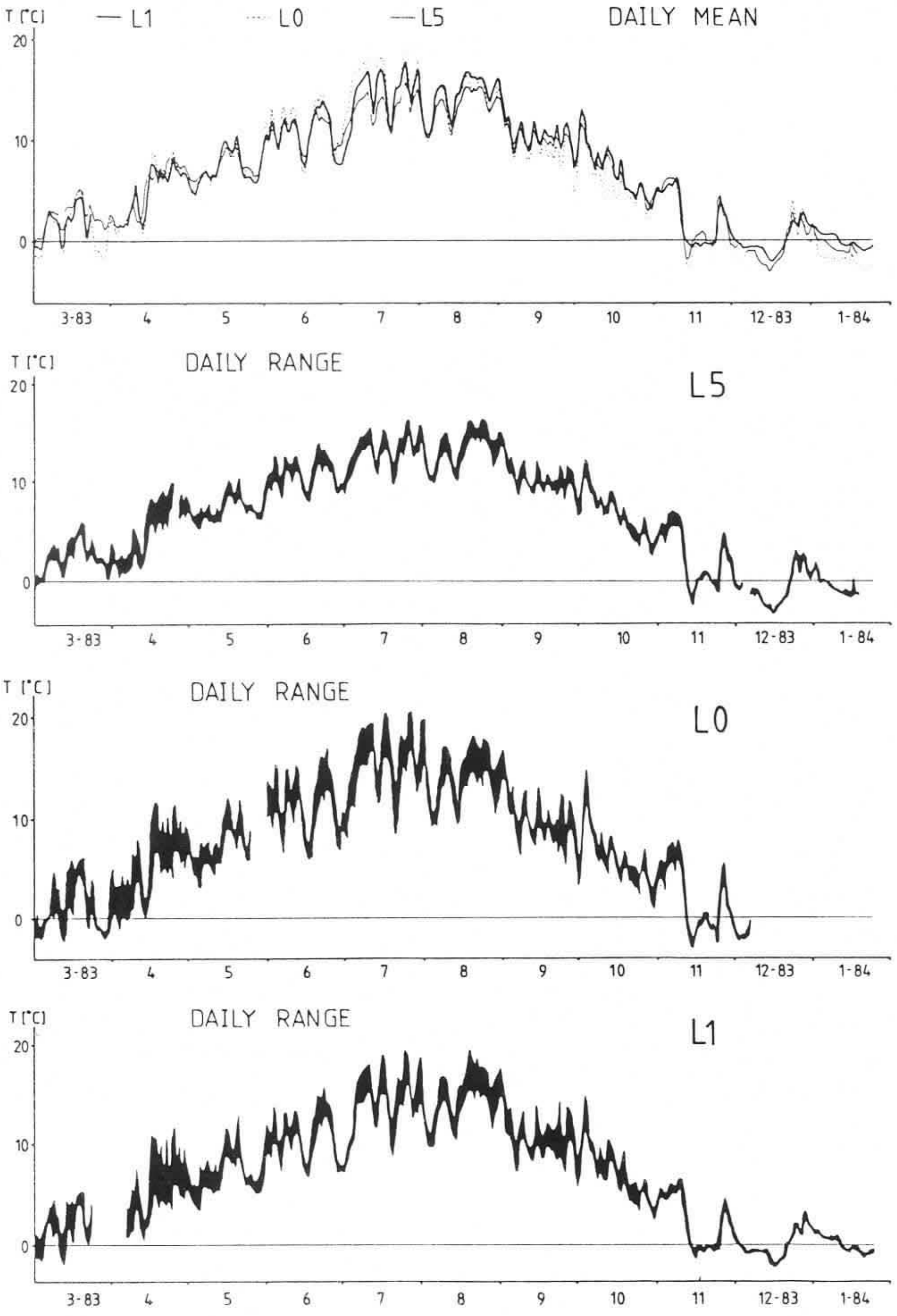


Fig. 3. Soil temperature regime of leaf litter manipulations L5 and L0, and controls L1: daily mean and daily minimum-maximum range of temperature at −1.5 cm in 1983/84.

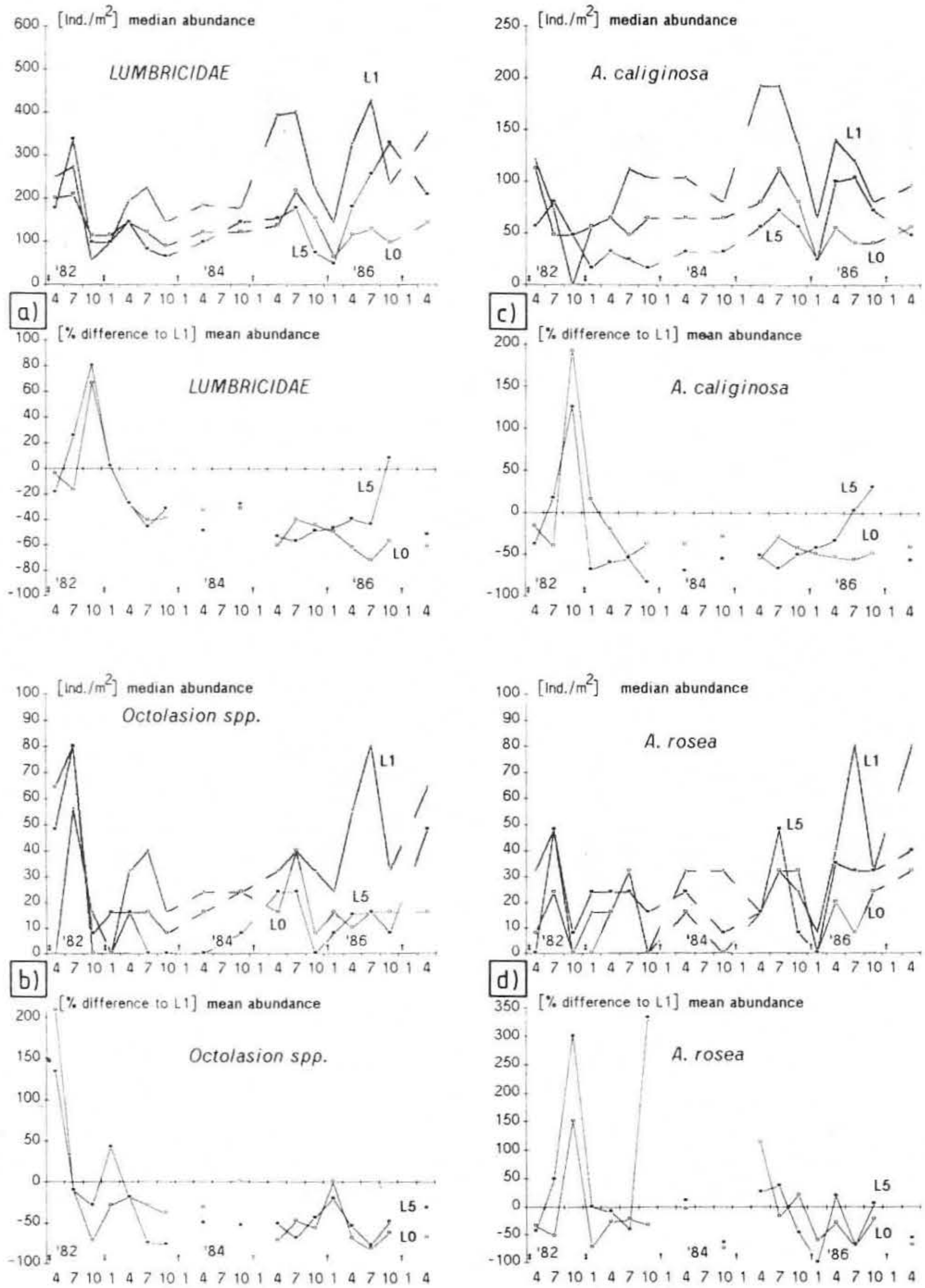
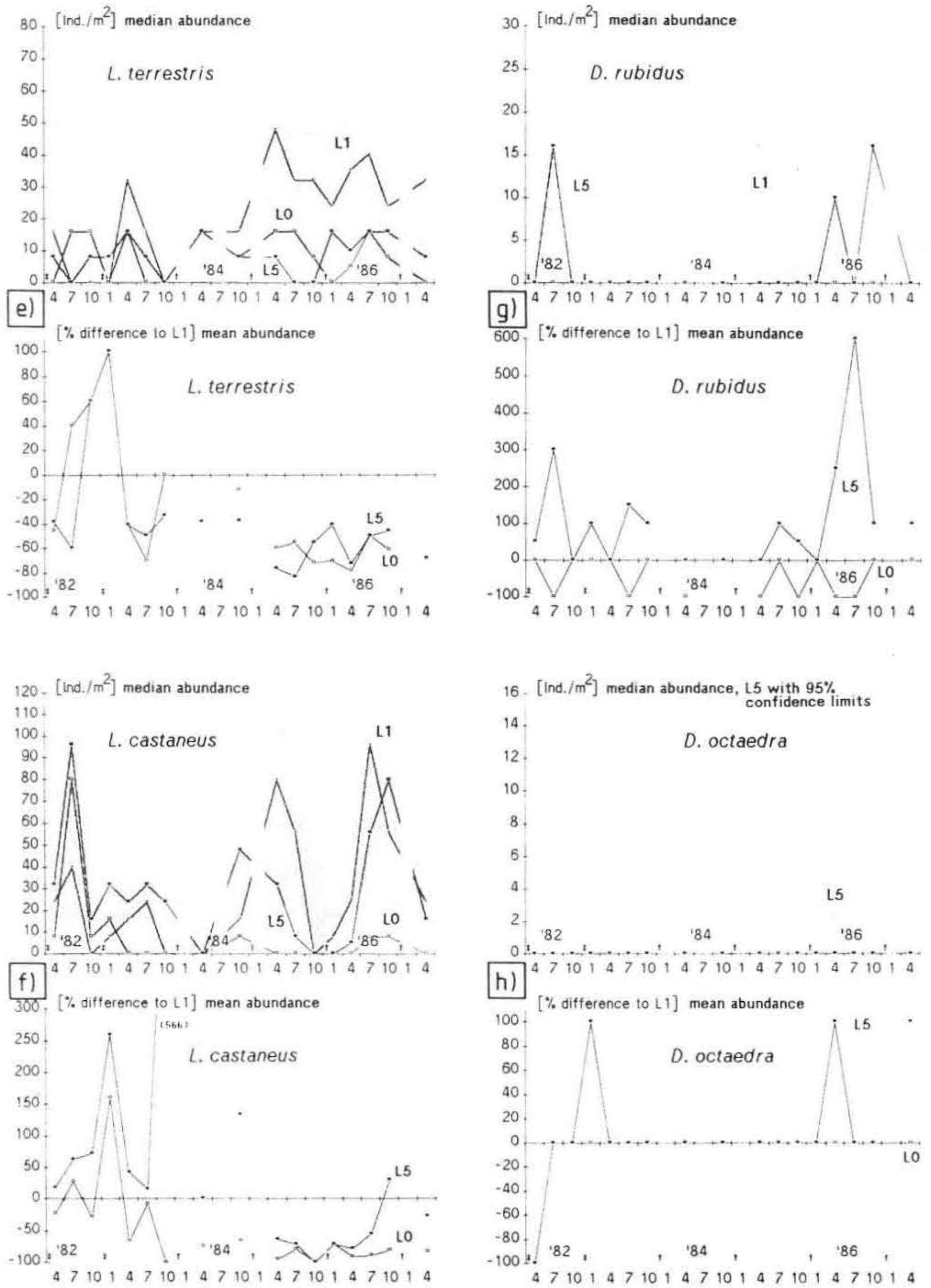


Fig. 4a–h. Development of earthworm populations following leaf litter manipulations, April 1982 to April 1987: (a) a l l species combined, (b)–(d) endogeic species [(b): *O. lacteum* and *O. cyaneum*], (e) anecic *L. terrestris*, (f)–(h) epigeic species. Upper figures: medians of abundance in control plots L1 (points), plots with litter exclusion L0 (open squares) and plots with litter multiplication (full squares), respectively; L1 with 95% confidence limits (shaded) [except for (h) *D. octaedra*]. Lower figures: percentage differences of mean abundances of L0 (open squares) and L5 (full squares) to L1, respectively [(f)–(h): if abundance of only one treatment was 0, percentage



difference was taken as +/− 100%]. Missing points and interruption of shading: no samples taken. Double arrows: dates of litter exclusion and litter multiplication, single arrows: dates of litter exclusion only.

3. Results

3.1. Abiotic parameters

The change of litter standing crop caused by the experimental manipulations (fig. 2c) was followed by a change of the abiotic environment. After one year, soil and litter water content (fig. 2a + b) tended to be higher for L5 and lower for L0 relative to controls. Daily and yearly variations of soil temperature were smoothed for L5 and pronounced for L0 (fig. 3).

3.2. Earthworm populations

In the first year of the experiment the abundance of all Lumbricidae (fig. 4a) displayed strong variations of manipulations about the control values. High percentage deviations were in part due to low absolute numbers. Since 4/83 L0 abundances remained lower than controls. L5 numbers declined also, with values often lower than L0. In the fifth year L5 abundances increased to L1 levels again, but correlations of both L0 and L5 with time are significantly negative (table 1). Average abundance relative to controls was for the whole experimental period of 4/82–4/87 66.3% for L0 and 74.9% for L5, and in 1986 39.7% for L0 and 69.7% for L5.

The **endogeic species** *Octolasion lacteum* (Örley) and *O. cyaneum* (Savigny) (fig. 4b) as well as *Aporrectodea caliginosa* (Savigny) (fig. 4c) showed trends similar to the all species' picture, although the increases in L5 in the last year are not as clear. *A. rosea* (Savigny) (fig. 4d) showed fluctuations of L0 and L5 values that are not different from controls.

Lumbricus terrestris L. (fig. 4e) was the only **anecic species** in the habitat investigated and its population had decreased in both L0 and L5 since 10/84, but absolute numbers were too small to be certain about the extent of the differences.

The dominant **epigeic species** *L. castaneus* (Savigny) (fig. 4f) nearly vanished from L0 from the second year on. In 1983 and 1984 its abundance was higher in L5 than in controls, but returned to the same level later on. This development causes a negative correlation of percentage difference with time (table 1). Absolute numbers of *Dendrodrilus rubidus* (Savigny) (fig. 4g) and *Dendrobaena octaedra* (Savigny) (fig.4h) were too low to give more than an indication of a decrease in L0 and an increase in L5.

Table 1. Summary of reactions of earthworm populations to manipulations of canopy leaf litter input in a beechwood on limestone relative to untreated controls.

	L0	R	L5	R
L. terrestris	–	-0.69^{2}	–	-0.50^{1}
L. castaneus	–	-0.68^{2}	(+)	-0.60^{1}
D. rubidus	–	0.05 ns	+	0.21 ns
D. octaedra			+	0.52^{1}
A. caliginosa	–	-0.64^{2}	(–)	0.08 ns
A. rosea	0	–0.08 ns	0	–0.39 ns
Octolasion spp.	–	-0.52^{1}	(–)	–0.47 ns
All species	–	$\mathbf{-0.89^{3}}$	(–)	$\mathbf{-0.53^{1}}$

L0: exclusion, L5: fivefold multiplication. "–": decrease, "+": increase, "0": no difference to L1, brackets: only for intermediate time interval. R: Coefficient of Spearman rank correlation of percentage difference of mean abundances with time; ^{3}: $P \leq 0.001$, ^{2}: $P \leq 0.01$, ^{1} $P \leq 0.05$, ns: $P > 0.05$.

The development of absolute and relative densities of earthworm species is summarized in table 1. All species but *A. rosea* decreased in L0 (no *D. octaedra* found). In L5, the anecic *L. terrestris* decreased, epigeics increased at least for an intermediate time interval, while endogeics except for *A. rosea* decreased during the same period.

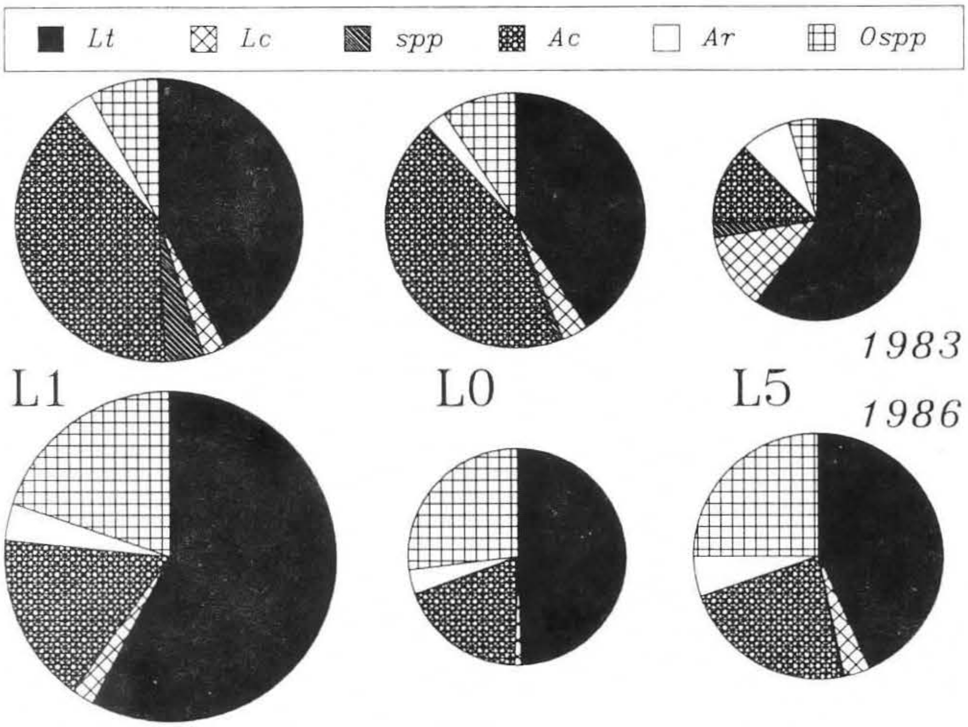


Fig. 5. Mean annual biomass of earthworm species following leaf litter manipulations. Means of 4 sampling dates (January, April, July, October) in 1983 and 1986, respectively, for the treatments L1 (control), L0 (exclusion) and L5 (multiplication), respectively. Area of circles and segments corresponds to absolute average biomass values; L1 in 1986 is equivalent to 10.9 g afdm/m^2, L5 in 1983 is equivalent to 4.2 g afdm/m^2. Species abbreviated by first letters of generic and specific names; spp: all other species.

The numeric reaction is reflected in biomass relations (fig. 5): L0 and L5 biomasses were lower than controls, *L. castaneus* nearly vanished from L0 and comprised a pronounced proportion of L5 biomass in 1983.

The intermediate increase of epigeic species and decrease of endogeics in L5 resulted in a marked shift of NORDSTRÖM & RUNDGEN's (1973) dominance index I_v to epigeic species (fig. 6). The L0-dominance was permanently shifted to endogeics after two years.

4. Discussion

The experimental exclusion of litter fall revealed that a natural litter layer is crucial for the maintenance of earthworm populations in the beechwood under investigation. However, the figures presented do not show whether the importance of an existing litter layer is due to the nutritive supply or due to the favourable abiotic conditions, namely higher humidity which it provides.

The increase of epigeic species following litter multiplication may be attributed to several functional factors: nutrition, abiotic variables like humidity, or simply an increase in microhabitat. Anyway, the litter layer seems to be the ultimate limiting factor for epigeic species.

The decrease of anecic and endogeic species is surprising and demands further investigation. At least, litter input is not a limiting factor for these species. The negative reaction to higher quantities of litter is interesting in the context that anecics and endogeics are missing in

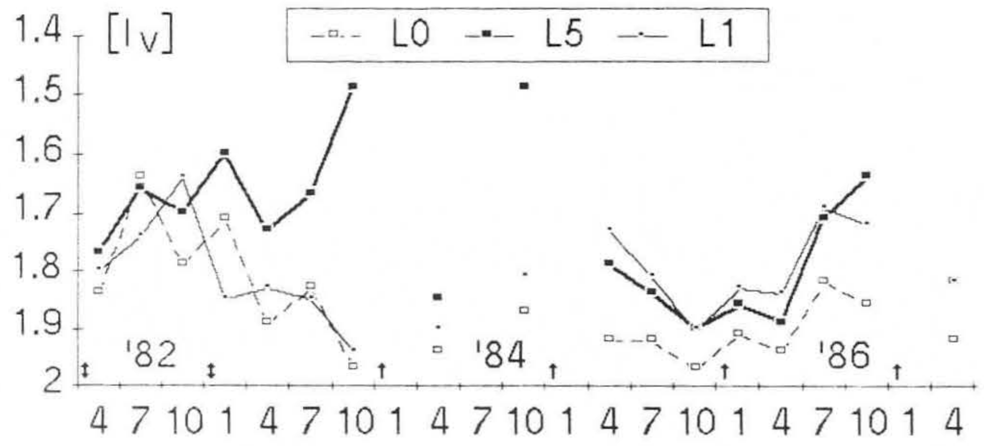


Fig. 6. Numeric dominance of life form types following leaf litter manipulations by exclusion (L0) or multiplication (L5). L1 = controls. The dominance index can take values between 1 and 2: I_v = (1*epigeics + 1.5*anecics + 2*endogeics)/(all individuals).

beechwoods with mor soils. Thus, these species may be restricted not only by soil acidity but also by factors connected with thick litter layers, such as oxygen supply or bacterial/fungal ratios perhaps. The increase of endogeics and the decrease of *L. castaneus* to control levels by the end of the experiment when the thick litter layer was degraded and resembled the natural layer confirm the adverse effects of excess litter on these groups.

Both experimental treatments showed *A. rosea* to be the species least affected by manipulations of the litter layer.

5. Summary

Following repeated exclusion of autumnal canopy leaf litter fall (L0) in a submontane beechwood on limestone, all species of lumbricid earthworms except *A. rosea* decreased.

A leaf litter input of 5 times the natural rate, repeated after one year (L5), caused a decrease of the anecic *L. terrestris*, epigeics increased at least for an intermediate time interval, while endogeics except for *A. rosea* decreased during the same period.

Average abundance relative to controls during the whole experimental period of 4/82–4/87 was 66% for L0 and 75% for L5. In the fifth year (1986) annual average abundance and biomass of all species was 40% and 43% of controls for L0 and 70% and 56% of controls for L5, respectively.

6. Zusammenfassung

Der wiederholte Ausschluß des herbstlichen Kronenlaubfalls (L0) in einem submontanen Kalkbuchenwald führte zu einer Abnahme aller Regenwurmarten außer *A. rosea*.

Ein Fallaubeintrag mit dem Fünffachen der natürlichen Rate, der nach einem Jahr wiederholt wurde (L5), bewirkte eine Abnahme des anözischen *L. terrestris*, epigäische Arten nahmen zumindest zwischenzeitlich zu, endogäische Arten, mit Ausnahme von *A. rosea*, zeigten eine vorübergehende Abnahme.

Für den gesamten Zeitraum des Experiments von 4/82–4/87 betrug die durchschnittliche Abundanz für L0 66% und für L5 75% der Kontrollen. Im fünften Jahr (1986) betrugen die Jahresmittelwerte von Abundanz und Biomasse für L0 jeweils 40% und 43% und für L5 jeweils 70% und 56% der Kontrollwerte.

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8. References

CONNELL, J. H., & E. ORIAS, 1964. The ecological regulation of species diversity. Amer. Nat. **98**, 399–414.

DIERSCHKE, H., & Y. SONG, 1982. Die Vegetation der Untersuchungsfläche des SFB 135 und ihrer Umgebung im Göttinger Wald. Kurzmitt. SFB 135 **1**, 3–8.

HURLBERT, S. H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. **54**, 187–211.

JUDAS, M., 1988. Washing-sieving extraction of earthworms from broad-leaved litter. Pedobiologia **31**, 421–424.

– 1989. Die Reaktion der Lumbriciden-Zönose eines Kalkbuchenwaldes auf experimentell veränderte Streumengen. Verh. Ges. Ökol. **17**, 251–256.

NORDSTRÖM, S., & S. RUNDGREN, 1972. Volumetric estimation of body size in lumbricids. Oikos **23**, 278–280.

– – 1973. Associations of lumbricids in Southern Sweden. Pedobiologia **13**, 310–326.

SCHAEFER, M., 1982. Zur Funktion der saprophagen Bodentiere eines Kalkbuchenwaldes: ein langfristiges Untersuchungsprogramm im Göttinger Wald. Drosera **'82**, 75–84.

Synopsis: *Original scientific paper*

JUDAS, M., 1990. The development of earthworm populations following manipulation of the canopy leaf litter in a beechwood on limestone. Pedobiologia **34**, 247–255.

In a submontane beechwood on limestone the development of earthworm populations following manipulations of canopy leaf litter input was studied for 5 years. Repeated exclosure of autumnal litterfall (L0) caused a decline in most species. Additional litter inputs of four times the natural rate at the beginning and in the first year of the experiment (L5) resulted in an overall decline, too, but epigeic species showed an increase for an intermediate time interval. In the 5th year the annual average abundance of all earthworms had decreased to 40% of controls for L0 and 70% of controls for L5, respectively.

Key words: Lumbricidae, population dynamics, beechwood, leaf litter, decomposition processes.

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